ON THE FERTILISATION OF *EUPOMATIA LAURINA*, R.Br.

By Alex. G. Hamilton.

(Plate III.)

This remarkable plant flowered plentifully in December, 1896, and I was able to make a series of observations upon it. The results fully support Robert Brown's hypothesis as to the method of fertilisation. He speaks of it in the following words :—"A singular part of the structure of *Eupomatia laurina* consists in its internal barren petal-like stamens which from their number and disposition completely cut off all communication between the antheræ and stigmata. This communication appears to be restored by certain minute insects eating the petal-like filaments, while the antheriferous stamina, which are either expanded or reflected, and appear to be slightly irritable, remain untouched. . . I have at least not unfrequently seen the barren stamina removed in this way, and as all the stamina are firmly connected at the base, and fall off together, it is difficult to conceive any other mode of exposing the stigmata to the influence of the antheræ" (1). In another place (2) he speaks of it in almost identical terms.

The late Dr. G. Bennett says :—"The *Eupomatia laurina* is found in woods and thickets about Port Jackson, and is abundant in the Illawarra district about the mountains. It flowers from December to February. The branches are long and drooping with handsome dark green laurel-like foliage, producing small white flowers of most singular structure and delightful fragrance. . . . In December the trees are covered with a profusion of white waxy flowers emitting an odor similar to that of *Magnolia fuscata*. The only insect I observed on the flowers was a small *Curculio* similar to that seen on the *Eupomatia* in Illawarra." In two footnotes he adds :—"Another species has been discovered in Moreton Bay District (Q.) with small but elegant variegated

flowers; it is figured in Sir Wm. Hooker's series of Curtis's Bot. Mag. Vol. 81, Pl. 4848, and Dr. Mueller, the Director of the Botanic Gardens at Melbourne, has done me the honour of naming it *E. Bennetti*. . . . The late Dr. Brown observed a singular part of the structure [Dr. Bennett here quotes the above passage]." In 1834 Dr. Brown requested me to observe in Australia the œconomy of these flowers, and to ascertain whether his statements were correct, and, if so, what insect is employed in the operation. On my friend Dr. H. visiting Illawarra, I desired him to make the necessary observations, as the *Eupomatia* was abundant in that district, and the only insect he found upon it was a small brown *Curculio*" (3).

In Curtis's "Botanical Magazine" (Vol. 81, t. 4848), *E. Bennetti* is figured and described under the name of *E. laurina*. The text says:—"The flower then, as seen in the figure, consists of a turbinate green receptacle, on the thickened edge of which the numerous stamens are arranged in many series, of which the outer are antheriferous, consisting of a broad subulate filament, with a linear cell on each margin, opening longitudinally; all the inner stamens are abortive, large, petaloid, obovate, yellow stained with orange or blood-colour at the base, especially the inner ones, and have exactly the appearance of a many-petalled corolla, of which the outer ones spread so as to cover and conceal the perfect stamens, while the inner ones are connivent, and almost conceal the ovaries. The outer of these petaloid stamens have the disc beset with conspicuous, stipitate globose glands, and the margin with stellated hairs, while the rest have both on the disc and the margin, stipitate glands. In Mr. Brown's plant, the petaloid abortive stamens are small and connivent, much shorter than the spreading fertile stamens, and destitute of the remarkable glands and stellated hairs" (4).

These are the only references I have been able to find to the peculiar structure of the flower, apart from descriptions in Fl. Aust. and Fr. Phy. It is figured in the Atlas to Brown's Botany of Terra Australis, t. 2, but I have not seen the figure.

The plant is a small tree growing plentifully near water-courses in Illawarra. The branches are long, thin and curved; the leaves light (not dark, as described by Brown) green with a varnished surface, oblong lanceolate in shape and recurving at the margins for a short distance above the petiole (figs 11 and 12); sometimes in leaves on young shoots from a felled tree, the fold forms a tooth (fig. 13). They resemble folds described as Domatia by Dr. Lundström in the oak and other plants, but I have not observed Acarids in them. "Sepals and petals completely consolidated into one mass, the upper part falling off in a conical lid, leaving the lower campanulate tube (or enlarged peduncle), filled with the thick flat-topped torus" (Bentham, Fl. Aust. i. p. 54). The stamens are of two kinds:—(1) The inner barren staminodia, broad, flat, and waxy, and described as greenish-yellow, but I have never seen them any other than ivory-colour. On the margins, in one or two instances, I have observed microscopic stellate hairs similar to those figured in the Botanical Magazine on *E. Bennetti*, but much smaller. These staminodes are in several rows, the inner rows leaning over the centre of the flower and entirely cutting off all access to it, the outer rows standing up all round (fig. 3, *s*). Outside of these is—(2) A row of fertile stamens, which in the bud are closely pressed together over the staminodia (fig. 2); but when the flower opens they gradually reflex till they reach a pendent position (fig. 3, *a*). The base of the filament is wide, thin, and concave, and when the open flower is touched, they move in a manner suggestive of irritability, as Brown pointed out, but I am certain that they are not sensitive in this way. The pollen grains are usually like a double-concave lens, but take other irregular shapes also (figs. 5 and 6). The carpels are many, and are inserted in the fleshy torus (fig. 8). The stigmas are sessile on the disc. When the flower opens, the whole of the disc and stigmas are moist, and I have not been able to make out whether they are then ready for pollination or not, but from the short time that the flower lasts, I imagine that they are in a fit state when it opens. The fruit is several-celled, formed of the enlarged calyx-tube, usually broadly turbinate, and about $\frac{3}{4}$ of an inch in

diameter. When ripe it is soft and purplish-red (fig. 7). The flowers are solitary in the axils, but frequently grow out from the trunk of the tree, a characteristic that belongs to others of the same natural order, as Wallace says of a *Polyalthia* in Borneo, that the slender trunk was completely garlanded with star-shaped flowers (5). *Ficus aspera* and *Castanospermum australe* have the same habit, which Wallace thinks belongs for the most part to tropical trees.

The flower opens in the early morning, and closes about 5.30 p.m. on the same day, the ring of staminodia and stamens dropping off entire the same night or early next day. These fallen flowers are very peculiar in appearance, quite unlike any blossom I have ever seen before. They resemble small sea-anemones more than anything else I can think of, and have a general uncanny appearance. The thin expanded bases of the filaments cause the stamens to tremble and wriggle in a way very suggestive of animal life. They have a very strong rich penetrating scent with reminiscences of other odours. Sometimes, as Bennett says above, it was like *Magnolia fuscata*, then one got a whiff of decaying pine-apple, and at times there seemed to be an intermingling of stale fish. A single flower in a room was quite sufficient to fill it with the perfume, and after handling the flowers, the smell clung persistently to the fingers. In previous years I had found stray blossoms at various dates from November to February, but in 1896 all the plants I could find flowered from the 18th to the 25th December, and after the latter date I could not find a single flower.

Having read what Brown and Bennett wrote about the insects frequenting the blossoms, I watched a tree near my residence for some time before it flowered, and specially searched for the Curculios, but could find none. On the 18th December I found two flowers open, but for a moment did not recognise them as flowers, as they were covered with a crawling mass of beetles. Yet the evening before I had examined the tree closely (it is a shrub of about eight feet in height) without discovering a single insect. When the branches were jarred, the beetles dropped off the flowers to the ground. Later in the day I again examined

the two flowers, and found that the beetles had eaten holes in many of the staminodia, and had penetrated to the heart of the flowers. On the discs rested a mass of débris, excrement and pollen-grains. The outer fertile stamens were untouched. The edges of the stamens and staminodes were turning a rusty brown. Next morning I found the two rings of stamens and staminodes beneath the tree, now rusty-coloured all over, as if decaying, but still emitting the characteristic scent. On this day—the 19th—no flowers were open, and again a careful search failed to reveal beetles anywhere on the plant. On the 20th December four flowers were open and covered with the insects, and on removing the central staminodes, I found several had penetrated to the disc. On the 21st almost every flower was open—some hundreds in number—and in every one I examined, the beetles were present on the outside, or within the staminodes—very often in both positions. As the day wore on, almost all of them disappeared, having made their way into the closed interiors. On visiting the tree at 9 p.m. I found that in almost all the flowers the fertile stamens had moved up to the bud position (fig. 2) covering the staminodes (which had also closed into the early position) closely. They were almost empty of pollen. In the morning almost all the previous day's flowers had dropped, and in these, as well as in the few which remained in place, the stamens were again in the reflexed condition and very limp, and the staminodes in the open position, but still cutting off access to the disc. One flower which I had protected from beetles before the operculum dropped was still open and in its place; on shaking it a cloud of pollen flew out of the stamens. The dropped blossoms on the ground were swarming with beetles, but there were none on the discs of the flowers which had lost their stamens. Microscopic examination of some of the insects showed that the tarsi, antennæ, and the hairs with which they are covered were dusted with pollen, so that any beetles making their way into the disc of a newly opened flower would be likely to bring about pollination.

Fertilisation appears to be effected by the beetles. These are attracted by the strong scent of the opening flower, and in alight-

ing on it, smear themselves with pollen from the fertile stamens, which at that stage have not reached the pendent position. They then bore into the disc through the staminodes, and continue eating the inner surface, at the same time placing the pollen on the stigmas. Thus it would seem that the first few flowers opening would certainly be self-fertilised. But all opening after the first day would be likely to be cross-fertilised, as the beetles would bring pollen from the flowers previously visited. Almost every flower on two trees which I watched has developed a fruit, a fact not be wondered at when the large number of beetles visiting the tree is considered.

When I first saw the beetles at work I was inclined to think that this was a case similar to the Yucca, in which the Yucca-moth stuffs the pollen into the hollow stigmas after depositing their eggs in the ovulary. But by careful observation I made sure that the bettles did not deposit their eggs about the flower, and that when the ring of stamens and staminodes dropped off, the disc was left clear of everything. And in sections since cut of large numbers of fruit, I have never found any larvæ. I am, therefore, quite certain that the process of fertilisation is as I have described it. A remarkable fact is, that notwithstanding the strong scent of some hundreds of blossoms on this tree, which was perceptible 20 yards away, no other insect visited them; although not far away there were hundreds of bees, butterflies, flies and other species of beetles at work on the blossoms of a myrtle bush. It would seem as if the plant deliberately laid itself out to attract the one species only.

The most important question arising out of this extraordinary method of fertilisation is how it could have originated. Here we have a flower so constructed as to cut off pollen from its stigmas completely, unless it is placed there by extraneous means. What were the steps by which the plant developed a large number of sterile stamens adapted—first, to cut off access of its pollen; and, second, to be attractive to beetles as food? And what first caused the beetles to visit the flower and so undo the self-imposed sterility of the plant? To these questions I am unable to offer any reply.

But a careful study of the structure of the stamens and methods of fertilisation in other plants of the Anonaceæ might reveal something of the line of evolution. It is the only plant of the Order with which I am acquainted; but on reading over the descriptions of the species of *Ancana*, *Polyalthia*, and *Melodorum* in Moore and Betche's "Handbook of the Flora of New South Wales," I found that in all these genera the connective of the anther is described as broad and flattened, concealing the cells. Here there may be a clue to the line of development. Might I draw the attention of botanists in Queensland and on our northern rivers to the desirability of observing the fertilisation of *E. Bennetti*? In this species the staminodes do not completely shut the disc up. It would be interesting to know if the same insect is concerned in the fertilisation, or an allied species.

The beetle (Fig. 10) which is to be described as a species of *Elleschodes* by the Rev. T. Blackburn in the next Volume of the Proc. Roy. Soc. of S.A. is one of the Curculionidæ belonging to the group Elleschides It is about 2 mm. in length, and possesses many adaptations to the flower. Thus it is provided with spurs on the inner aspect of the tibiæ of the two front pairs of legs, and a comb-like series of points along the tibiæ where the tarsi are attached. These enable it to cling to the slippery surface of the staminodes and give it a firm hold as it forces its way into the head of the flower. From its hairiness, it is well adapted to carry the pollen from one flower to another and thus to ensure cross-fertilisation.

References.

(1) Brown, R.—Miscellaneous Botanical Writings, Vol. i. p. 74.

(2) „ „ —Botany of Terra Australis, p. 65; Atlas, t. 2.

(3) Bennett, Dr. G.—Gatherings of a Naturalist, p. 363.

(4) Curtis—Botanical Magazine, Vol. 81, t. 4848.

(5) Wallace, A. R.—Tropical Nature, p. 35.

EXPLANATION OF PLATE.

Eupomatia laurina, R.Br.

Fig. 1.—An unopened bud.

Fig. 2.—Bud after the fall of the cap.

Fig. 3.—The open flower ; *a*, fertile stamens ; *s*, staminodes.

Fig. 4.—A stamen.

Fig. 5.—Pollen grains—dry.

Fig. 6.—Pollen grain in clove oil.

Fig. 7.—The fruit.

Fig. 8.—Longitudinal section of fruit.

Fig. 9.—Transverse section of fruit.

Fig. 10.—The beetle (*Elleschodes* sp.).

Figs. 11-13.—Bases of leaves, showing the folds.